

Relationship between wild and cultivated yams: Case study of yam domestication in Benin

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Abstract

The *Dioscorea cayenensis* – *Dioscorea rotundata* species complex is the most widely cultivated yam in West Africa. It has been described as deriving from wild types belonging to the species *Dioscorea abyssinica* and *D. praehensilis* from *Enanthiophyllum* section, through domestication by African farmers. Wild types were chosen on the basis of morphological criteria. In order to translate farmers' knowledge into standard descriptors and to assess whether domestication has a genetic base or not, 140 accessions of wild types *D. abyssinica* and *D. praehensilis* were collected in Benin. They were studied using IPGRI's yam descriptors, highlighting a continuum between the two species. A structuration of both species into domesticable and non-domesticable yams was observed. Based on 10 nuclear DNA simple sequence repeats (SSR), the molecular characterization leads to separation of *D. abyssinica* species into domesticable and non-domesticable groups. To establish phylogenetic relationships existing between wild and cultivated species, we investigated changes in chloroplast DNA simple sequence repeats (cpSSR) in a second collection compiled by 148 accessions selected to cover the genetic diversity existing in Benin. *Dioscorea cayenensis* and *D. rotundata* shared the same haplotype. The morphotype *abyssinica* appeared to be subdivided into 3 haplotypes from which one is shared with the *D. cayenensis*–*D. rotundata* species complex and with *praehensilis* morphotypes, suggesting that they might belong to the same species. Some taxonomic changes within the *Enanthiophyllum* section were suggested. *Dioscorea minutiflora*, *D. smilacifolia*, and *D. burkilliana* might also be suspected to belong to the same genetic group.

Keywords : yam, domestication, phylogeny, farmers' knowledge.

Introduction

In West Africa, yam is a very important component of cropping systems and food security. Yam is not only an important preferred food but an indigenous crop tied up with the cultures and tradition of the people in the so-called *yam belt* which stretches from Côte d'Ivoire to western Cameroon.

The most cultivated species, which accounts for nearly 95% of the world's yam production (FAO, 2004), are the *Dioscorea cayenensis* (Lam.)-*D. rotundata* (Poir.) species complex (also referred to as Guinea yam) belonging to the section *Enanthiophyllum*. Guinea yams have been described according to different authors as resulting from a process of domestication of wild yams *D. praehensilis* Benth. and *D. abyssinica* Hochst ex Kunth from the section *Enanthiophyllum* by African farmers (Dumont 1998, Scarcelli et al. 2006) and this opinion is supported by genetic studies (Ramser et al. 1997, Mignouna and Dansi 2002).

Field surveys which were recently undertaken in Benin and Nigeria have shown that the process of domestication is still ongoing (Mignouna and Dansi 2003; Vernier et al. 2003). Small-scale farmers mainly acquire new cultivars from their neighbours, during travels or by

collecting tubers found in fallows or forests. The performance of a new cultivar within the local environment and farming system determines whether it will be adopted then cultivated. According to farmers, some of these plants develop after 3-6 years of special cultivation practices—a tuber that is morphologically close to those of cultivated varieties. The tubers are then multiplied and cultivated if their morphology is convenient to farmers. The biological process underlying the change in tuber morphology during domestication and its maintenance over next generations is unknown (Scarcelli et al. 2006).

Yam domestication represents a remarkable case of a farmer-driven process of plant breeding with a vegetatively propagated crop. It appears to take advantage of the huge reservoir of biodiversity preserved in wild yam populations. Cultivated varieties represent a rather limited range of genetic diversity for varietal improvement due to the vegetative propagation of yams (Scarcelli et al. 2006).

In Benin, data on yam domestication have shown that the practice in Bariba group from the north is about 3.7% of farmers (Baco 2000). In the region of Bante, at the centre of Benin, Okry (2000) estimated the percentage of domestication as 9.2%. In the Nago and Fon area, Mignouna and Dansi estimated the percentage of domestication as nearly 5%.

It is also shown that current practices of domestication are tending to decline, especially where yam production is mostly market-oriented, and this endangers the future of *D. rotundata*, a species representing about 90% of yam production in the world, and which is a major component of food security in Africa (Vernier et al. 2003).

Although the importance of domestication in broadening of existing genetic diversity (Mignouna and Dansi 2003), no studies were conducted to link the farmers' knowledge to scientific parameters in order to understand and reproduce the domestication process and to assess the genetic diversity among wild yams.

Also, little is known about the phylogeny of Guinea yam and many taxonomic ambiguities are still remaining. It is assumed that by combining data gathered from both field surveys and molecular analysis, progress could be made in the way of clarifying relationships between cultivated *D. cayenensis*-*D. rotundata* and its putative wild relatives, namely *D. praehensilis* Benth. and *D. abyssinica* Hochst ex Kunth.

In the present study, we will attempt to “translate” farmers knowledge into morphological markers based on IPGRI descriptors (IPGRI/IITA 1997) and using nuclear SSR markers developed on yam (Tostain et al. 2006) to investigate if such classification has a genetic basis. Our aims also were to investigate the phylogeny of *D. cayenensis*-*D. rotundata* species complex, and to provide information on the relationship between: i) *D. cayenensis*-*D. rotundata* and their putative parents *D. abyssinica* and *D. praehensilis*; and ii) cultivated yams and other yam species found in Benin.

Material and Methods

Survey and sampling strategies A participative approach was used for sampling. The farmers domesticating yam were subjected to an interview according to a questionnaire. The questions focused mainly on the kind of wild material used for domestication, the areas where these wild yams were collected, and the selection criteria used during the process. The surveys were conducted in regions selected according to the geographical distribution of *D. abyssinica* (north) and *D. praehensilis* (south) in Benin. These two species are sympatric in the Centre. The surveys were carried out during two periods, on June and on November 2004. The

collecting sites were the forest of Ouenou-Benou and Trois rivières (in the north); the forest of Toui-Kilibo (in the centre); and the forest of Lama, Ewe, Sozoun, Hizihan, Bozoundji and Lanwlixa (in the south). Tubers were identified as domesticable or not by farmers. On the whole, 128 tubers were collected. The accessions include *D. praehensilis* (19 and 18 accessions farmers identified as domesticable and non domesticable respectively) and *D. abyssinica* (53 domesticable and 38 not domesticable). An additional survey was carried out in the Goungoun forest and the hunting zone of Djona located beyond the 12th parallel, area where the farmers do not cultivate yam. Eleven accessions considered as true wild types of *D. abyssinica* were collected in these areas, where it is supposed that yam has never been cultivated. The last and one accession of *D. togoensis* was used as control.

For phylogeny studies, tubers were collected during the yam harvest period, between November and December in years 2001 and 2002 at Yarra, Wari, Fo-Boure and Gorobani villages (North), at Banon, Loughba, Djagballo and Galata villages (Centre) and at Djaloukou, Konkondji, Lahongbon, Gohougbehoue and Djidja villages (Centre). A total of 148 clones were collected, consisting of i) cultivars of the *D. cayenensis*-*D. rotundata* species complex including accessions of cultivars Ikeni from the ALAKISSA cultivar group, classified as *D. cayenensis* Lam., ii) yams under domestication at different steps (years of cultivation) considered as intermediate between cultivars and wild types (*D. abyssinica* and *D. praehensilis*) and, iii) representatives of *D. abyssinica* and *D. praehensilis* populations collected in forests (either close to the farmer fields or far from them). To establish the phylogenetic relationship between cultivated yams and wild yams, accessions of wild types from other species found in Benin were also included in this study, such as *D. togoensis* Knuth, *D. bulbifera* L., *D. minutiflora* Engl., *D. smilacifolia* De Wild, *D. burkilliana* J. Miège., and *D. dumetorum* Pax. (Contedge, a cultivar of this last species was also included). One accession of *D. alata* L., a species described as originating from Oceania but belonging to the section *Enanthiophyllum* and introduced in Africa during the 16th century (Hahn, 1995), was added to the sampled populations. Collected tubers were planted in the experimental field for *ex-situ* preservation at the University of Abomey-Calavi in Benin in February 2002. Leaves were sampled for molecular analysis in May and June 2002.

Morphological analysis All collected tubers for domestication study were field planted at the University of Abomey-Calavi. They were morphologically described using the descriptors highlighted by IPGRI (IPGRI/IITA 1997) as the most pertinent for the identification and description of yams. Aerial vegetative parts were monitored between April and August 2004. Tubers were harvested only once at the end of January and were described immediately.

Simple sequence repeats marker analysis DNA extraction was performed as described in Chair et al. 2005. For the genetic analysis, 10 nuclear microsatellites markers: Da1G12, Da2F10, Da1F07, Dab1C12, Dab2D11, Da1A01, Da1D08, Dab2C05 and Dab2D08, (Tostain et al. 2006) were amplified. For phylogeny analysis, four *Nicotiana tabacum* Chloroplast SSR (NTCP8, NTCP9, NTCP37, NTCP39 and NTCP40) previously developed by Bryan et al. (1999) and one consensus chloroplast microsatellite (ccmp 2) isolated in tobacco by Weising and Gardner (1999) were used.

Data analysis Each morphological character was scored as a Bernoulli variable (0, 1). If a character was present, it was scored 1, if absent 0. Using this methodology, 44 morphological descriptors were created. The frequency of descriptors in each group of domesticable and non domesticable within *D. abyssinica* and *D. praehensilis* was calculated (Number of accessions having the modality/Number of accessions of the species) x 100. Only discriminant

descriptors were retained for the analysis. Factorial Analysis on Dissimilarity (FAD) was performed using dice index and computed with Darwin software (Perrier et al. 2003).

Microsatellite analyses were performed using allelic data. A Neighbor Joining Tree (NJTree) (Saitou and Nei, was constructed on a dissimilarity matrix (Dice index) and computed with Darwin software (Perrier et al. 2003). Phylogenetic studies were performed as described in Chair et al. 2005.

Results and Discussion

Farmers' knowledge on domesticable/non domesticable yams In the north, the interviews lead to the identification within *D. abyssinica* of 4 different morphotypes of domesticable and one of non-domesticable yams. The domesticable yams are:

- Digui Teingni. The tuber, close to the soil surface bears many roots. The stem is slightly spiny;
- Digui Waaha. The tuber is very long, without roots, bearing many calli and growing at approximately 40 cm from the soil surface. The stem is slightly spiny.
- Digou Wongourou. The tuber, at the soil surface bears strong roots at the head and small roots at the « tail ». Its spiny stem at the lower part is bearing cataphylls oriented toward the bottom ;
- Worou Dogorogou. The tuber is very long grows nearly at the soil surface, bearing strong roots at the head and small roots at the « tail ». The spiny stem at the lower part bears cataphylls directed upward.

The unique morphotype of non domesticable yam is named Dika Yamberekou. The farmers identified it by the very big size of the leaves with different shapes and very distinct lobes. The stem is slightly spiny and is bearing very small cataphylls. The tuber is generally very small in diameter and very elongated. It possesses rarely roots. But observations on the field let suppose that confusions often occur between this morphotype and *D. togoensis*.

In the centre, farmers domesticate more frequently *D. abyssinica* than *D. praehensilis*. According to them, there is one morphotype of domesticable *D. abyssinica*. The characteristics of stem, leaves and tuber are various but correspond to those of *D. abyssinica*. The non-domesticable yams were identified as *D. dumetorum*, *D. togoensis*, *D. hirtiflora*, *D. smilicifolia*, *D. bulbifera* and *D. preussi*. These farmers do not recognise non-domesticable *D. abyssinica*. They give the name of « Itchou Igbo" to all wild yam species.

In the South of Benin, the existence of 2 morphotypes into *D. praehensilis* is accepted even if the criteria of discrimination are not shared between all the farmers. The domesticable morphotype of *D. praehensilis* in Nago and Fon area is named "Dohoun Assi". The farmers recognise its stem of small diameter (around 0.5 cm) bearing spines with variable lengths and cataphylls. The tuber has white flesh, is poor in fibres and protected, at its top, by a small crown of spiny roots. The non-domesticable morphotype « Dohoun Assou » presents very spiny stem with a large diameter (average 1 cm). Spines are very long and generally curved. Cataphylls have also very big size. The tuber presents a reddish flesh very rich in fibres. It is protected by a strong crown of spines which can reach the soil surface.

During this survey, *D. abyssinica* appeared more represented than *D. praehensilis*. Also, it was found that a few farmers domesticate yam. However, farmers from the North, especially from Zougou-Pantrossi, Dougoulayé and Fô-Bouré have more domestication skills.

Morphological characterisation of domesticable/non domesticable yams The morphological characterisation based on IPGRI descriptors has lead to 3 classes of characters in our sample: monomorphic, slightly polymorphic and highly polymorphic. We have chosen to consider only the highly polymorphic characters.

The analysis, excluding tubers traits, has shown that the difference between domesticable and non-domesticable yams is based mainly on the stem characters. The non-domesticable *D. praehensilis* have a stem with very large diameter, very long spines and well developed cataphylls in comparison with the domesticable ones and with the *D. abyssinica* yams. Concerning *D. abyssinica*, the domesticable yams have a stem covered with prune and spines of medium size. In comparison, the non-domesticable *D. abyssinica* have a stem bearing little pruned and very short spines.

Using the descriptors considered, a FAD was drawn. The plan 1-2 (Figure 1a) separated the *D. abyssinica* domesticable from non-domesticable. Nevertheless, 3 accessions of non-domesticable *D. abyssinica* among 40 accessions were found among domesticable ones and 9 among 36 domesticable yams were within non-domesticable ones.

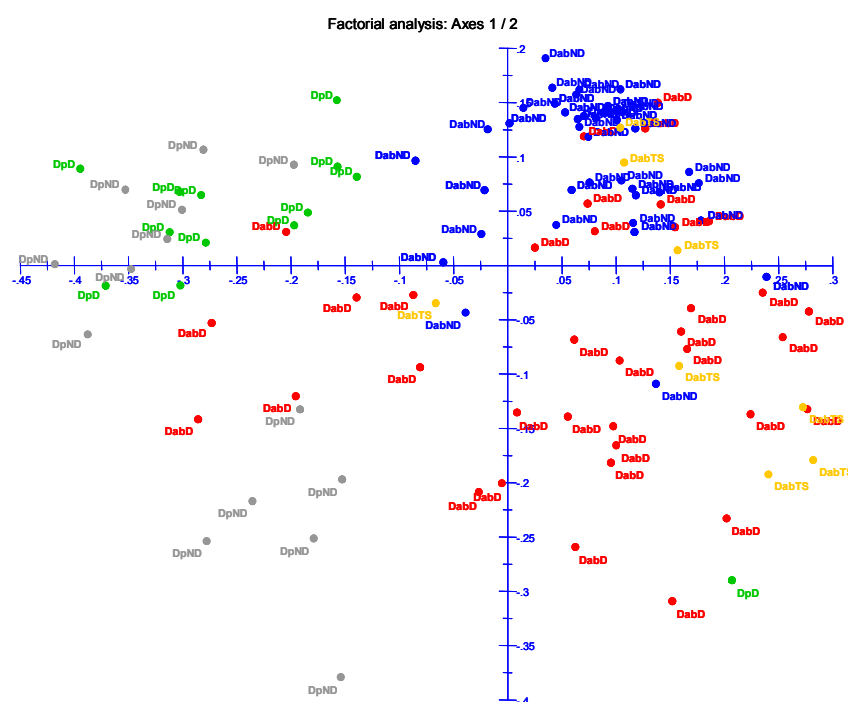


Figure 1a: FAD using IPGRI descriptors to discriminate between domesticable and non-domesticable yams in *Dioscorea abyssinica* and *D. praehensilis* species. Plan 1-2

The plan 1-3 (Figure 1b) displayed a high separation between *D. praehensilis* domesticable and non-domesticable, excepted 3 accessions of domesticable yams which are found among the non domesticable ones and 2 accessions of non-domesticable which are found among domesticable. The discriminant character between domesticable and non domesticable *D. praehensilis* is based essentially on the spines around the head of tubers. This character is more attenuated when *D. praehensilis* is considered as domesticable.

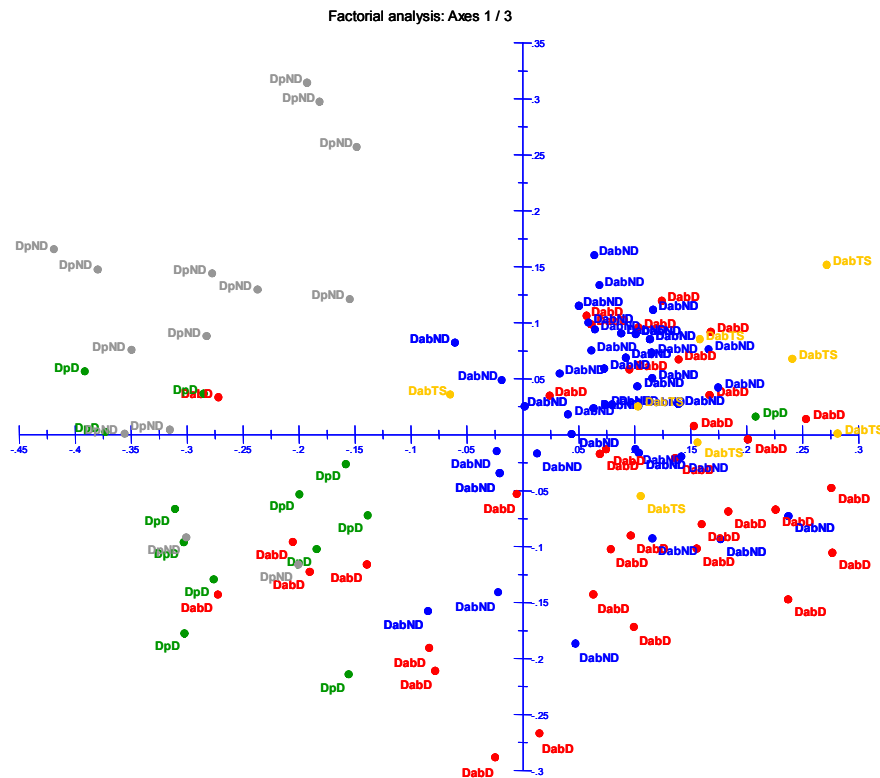


Figure 1b: FAD using IPGRI descriptors to discriminate between domesticable and non-domesticable yams in *Dioscorea abyssinica* and *D. praehensilis* species. Plan 1-3

During surveys, a special attention has been given to the selection of farmers. Only old farmers skilled on domestication were chosen, but even if they master the process, domestication is not always successful. Since farmers use mostly aerial criteria for domestication, discriminating characters are not always obvious. And sometime, they fail to obtain edible yam after many years of domestication. This can explain that a few accessions are not classified in the group in which they were expected to be.

Nevertheless, with an acceptable accuracy, farmers' knowledge is translated into morphological descriptors which may help in the choice of wild yams *D. abyssinica* and *D. praehensilis* for initiation of the domestication process.

Molecular characterisation of domesticable and non-domesticable yams

Nuclear SSR markers: Nine among the 10 SSR markers were retained. Da1D08 was removed due to a too high number of missing data. The NJTree obtained based on these markers display a high separation between *D. abyssinica* and *D. praehensilis* (Figure 2). The structure of the NJTree is correlated neither with the collect area nor with the ethnic group.

The mean number of alleles per locus ranged from 5.8 to 9. It is higher in *D. abyssinica* than in wild type *D. abyssinica* -collected beyond the yam culture area- and in *D. praehensilis*. This could be related to the number of accessions collected. In our survey, we collected more *D. abyssinica* than *D. praehensilis* reflecting that way the situation of *Dioscorea* spp. in Benin. *D. abyssinica* is located in the north which is a very broad area in comparison with the south. The accessions were collected from large areas which may explain their high mean number of alleles per locus. The accessions of wild type *D. abyssinica* were all collected in Gogoun forest, which limits in spite of their sexual reproduction mode, their genetic diversity. Gogoun forest in this case could be considered as a niche with more homogeneous genotypes.

D. praehensilis is found primarily in the humid forest galleries of the south. However, forests are in the process of degradation in Benin cause of the high demographic pressure which put *D. praehensilis* under genetic erosion decreasing its genetic diversity.

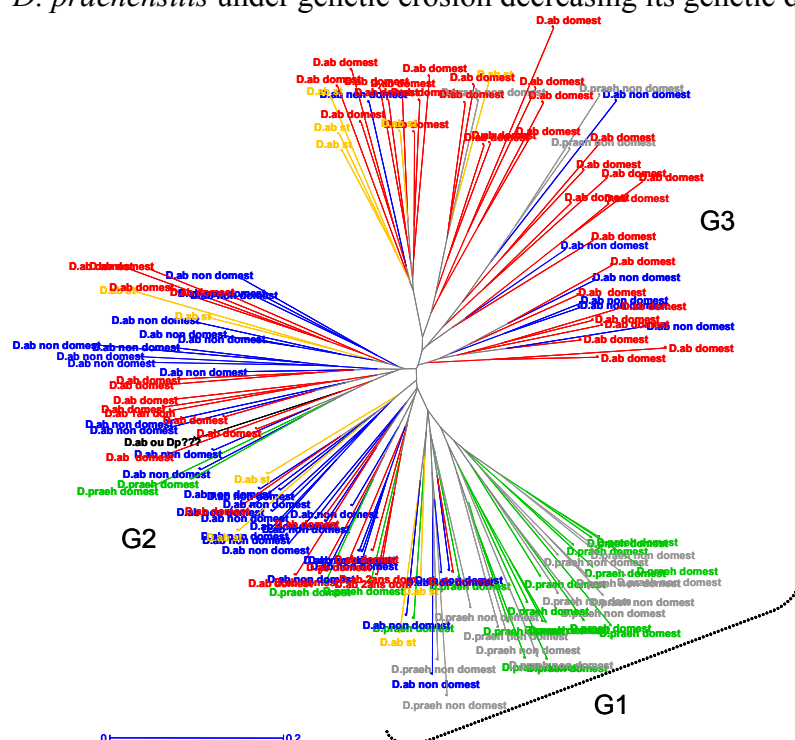


Figure 2: Dendrogram based on nuclear SSR dataset of 145 accessions of *D. abyssinica* (D.ab) and *D. praehensilis* (D.praeh) described as domesticable (domest) or non-domesticable (non domest) according to farmers and wild type of *D. abyssinica* (st).

In the NJTree, *Dioscorea praehensilis* accessions form a distinct cluster (G1) including domesticable and non-domesticable yams. In G1, we can distinguish a heterogeneous sub group which is closer to cluster G2. In addition to *D. praehensilis*, the sub group contains 3 accessions of non domesticable, one accession of domesticable and 2 accessions of wild type *D. abyssinica*. These accessions could hardly belong to *D. praehensilis* species. Indeed, according to morphological data's, these accessions are classified well in *D. abyssinica* group. In this study, if the identification of domesticable/non domesticable yams were made by the farmers, we carried out ourselves the assignment of accessions to one of 2 species *D. abyssinica* or *D. praehensilis*.

The second cluster (G2) is mainly constituted by non domesticable *D. abyssinica*. It contains also 4 accessions of domesticable *D. praehensilis*, 17 accessions of domesticable *D. abyssinica* and 3 accessions of *D. abyssinica* WT. This rather heterogeneous group is closer genetically to the cluster of the *D. praehensilis* than the cluster 3 of mainly domesticable *D. abyssinica*. In G2, only 2 accessions considered as *D. abyssinica* domesticable are also found in the morphological data among *D. abyssinica* non domesticable and only one *D. praehensilis* domesticable is found among *D. abyssinica* domesticable. The other accessions are well classified according to their morphological group.

A third cluster (G3) formed mainly of *D. abyssinica* domesticable but which contains also seven accessions of *D. abyssinica* non domesticable and 2 accessions of *D. praehensilis* non

domesticable. These 2 last accessions are well gathered with *D. praehensilis* non domesticable after morphological analysis.

SSR data enable us to separate the *D. abyssinica* from *D. praehensilis* accessions which is in agreement with the result obtained by Scarcelli (2006). In this study, we also obtained a separation between domesticable/ non domesticable *D. abyssinica*, whereas *D. praehensilis* cannot be separated. This discrimination rests primarily on 5 rare alleles out of 4 loci which are specific of domesticable *D. abyssinica*.

Chloroplastic SSR markers: Using cp-SSR markers, we analysed the same sample. Only, NTCP8, NTCP9 and ccmp2 displayed polymorphism within the collection (Figure 3). We obtained 3 major clusters: The first cluster (haplotype 1) encompasses *D. abyssinica* domesticable and both domesticable and non-domesticable *D. praehensilis*. The second cluster (haplotype 2) group accessions of *D. abyssinica* non-domesticable, of wild type *D. abyssinica* collected beyond the yam culture area, two accessions of domesticable and only one accession of non domesticable *D. praehensilis*. Finally, a third cluster (haplotype 3) regroupes the majority of non-domesticable *D. abyssinica*.

The same markers were used to conduct a study on the second sample which contains also accessions of *D. cayenensis-D. rotundata* (data not shown). The results did not show any difference between accessions of *D. cayenensis-D. rotundata* and most of the accessions of the two wild species *D. abyssinica* and *D. praehensilis*. An exception has been observed with four accessions of *D. abyssinica* which form a distinct haplotype and differ from haplotype 1 for two loci out of five. They are either wild type, or yams considered as potentially domesticable by farmers, or yams under domestication. Assuming that the phylogenetic signal given by these cpSSR markers is accurate, we may cautiously hypothesize that these five accessions as well as haplotypes 2 and 3 in the first analysis are belonging to a distinct genetic group. It is difficult to consider these 2 haplotypes as distinct species. Since, even if the same accessions form distinct genetic group after nuclear analyses, they still share most alleles with *D. abyssinica* domesticable. Other yams sharing haplotype 1 described as being *D. abyssinica* or *D. praehensilis* might be considered as morphotypes of *D. cayenensis-D. rotundata* cultivars, which escaped in forests or in ancient bush, originating from either seed germination or sprouting of remaining tuber fragments after harvesting. Then the morphological plasticity may be invoked to explain a fast reverse by adaptation to environment toward wild form usually qualified as *D. abyssinica* in savannah conditions or *D. praehensilis* in moist forests.

In this study, all accessions of *D. praehensilis* share haplotype1 and no distinct haplotype was isolated. It may be related to the scarcity of chloroplastic markers we used, or considering the previous hypothesis, *D. praehensilis* could be seen just as a wild morphotype of a large compartment including *D. cayenensis-D. rotundata* cultivars, wild *D. abyssinica* and *D. praehensilis*.

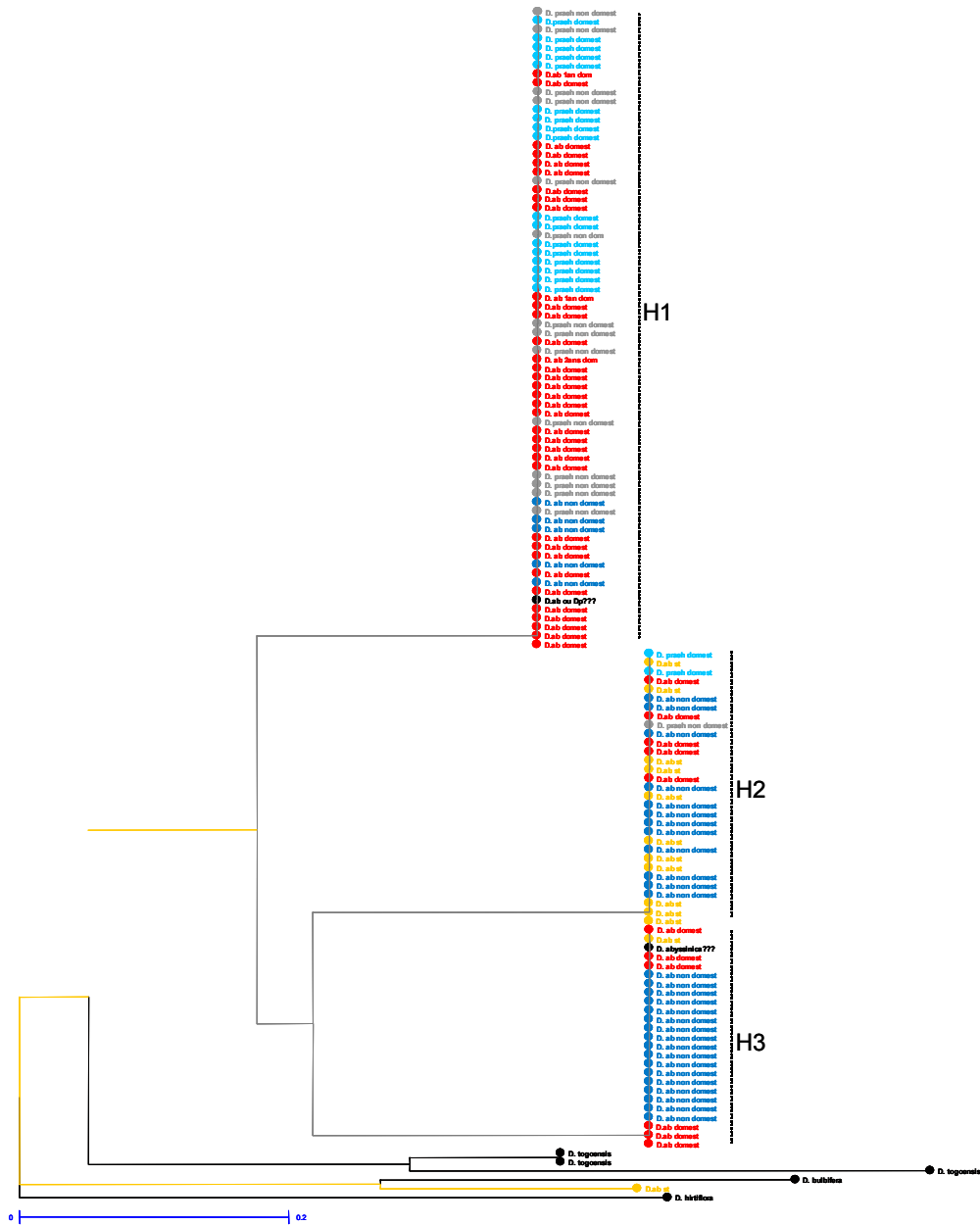


Figure 3: Dendrogram based on cpSSR dataset of 145 accessions of *D. abyssinica* (D.ab) and *D. praehensilis* (D.praeh) described as domesticable (domest) or non-domesticable (non domest) according to farmers and wild type of *D. abyssinica* (st). *D. togoensis*, *D. bulbifera* and *D. hirtiflora* were used as outgroups.

In this work, we could translate the farmers' criteria corresponding also to farmers' knowledge into morphological criteria. Few discriminating characters were highlighted but they are enough to separate domesticable from non domesticable yams for the two species. It is the first time that such work is done. To fill in the data set, other criteria of discrimination should be developed.

The molecular data analysis using nuclear SSR, enabled us to identify 2 genetic groups corresponding to the species *D. praehensilis* and *D. abyssinica*, which is in agreement with Scarcelli et al. 2006. We did not introduce *Dioscorea cayenensis* – *Dioscorea rotundata* into this analysis, since our focus was especially on domestication criteria determination and it

was already done by Scarcelli. For the first time, a genetic group of domesticable yams could be separated with nuclear data. This group is distinguished from the other *D. abyssinica* by only 5 rare alleles. This work should be repeated to be validated.

Lastly, these results join those obtained with the chloroplastic data, where a haplotype *D. cayenensis* – *D. rotundata*, *D. abyssinica* and *D. praehensilis* was found and 2 haplotypes of non domesticable *D. abyssinica* could be separated. We suppose that the complex *D. cayenensis* – *D. rotundata*, *D. abyssinica* and *D. praehensilis* forms only one species or one genetic group whereas the state of non domesticable *D. abyssinica* group remains uncertain. They might be considered as distinct genetic group based on their chloroplastic genome. It is difficult to regard them as distinct species because, on nuclear data basis, they share several alleles with domesticable *D. abyssinica*.

In both studies, we did not highlight a distinct haplotype of domesticable or non domesticable *D. praehensilis*. Yet in our study, we had only 3 tobacco cpSSR markers to discriminate the different haplotypic groups. Either, with more markers, may be yam specific, they could be separated, or there is no separation and in this case one can suppose that there is no genetic determinism of domestication for *D. praehensilis* yams. More investigation are needed to understand why in the case of *D. abyssinica*, we manage to discriminate domesticable/non domesticable yams whereas for *D. praehensilis* we did not find up to now any genetic determinism of domestication. New molecular markers can be used but, more important is to assess i) the farmers choices a posteriori by supervising which yams were really successfully domesticated, ii) if the existence of different cytoplasms of *D. abyssinica* in sympatry is related to any effect of human selection pressure. Lastly, if any relationship is confirmed, it remains to explain the cytoplasmic mechanisms which influence phenotypical plasticity.

Evolution between and within *Dioscorea* species The four sections represented in this analysis are clearly separated (Figure 4). Some points of interest could be highlighted. In the section *Enantiophyllum*, the haplotype H1 including all cultivars and *D. abyssinica* or *D. praehensilis* wild forms is partially linked with representatives of *D. smilacifolia*, *D. minutiflora* and *D. burkilliana* that share the same haplotype H2. According to these results, these three species might be considered as one “genetic group” who diverged later from other *Enantiophyllum* species. As they were found in the same habitat, questions related to the co specificity of these species could be addressed.

Dioscorea togoensis (H3) is an uncertain species found only in West Africa and presents a small genome (Hamon et al. 1992) which may suggest that it has diverged later from other *Enantiophyllum* species. Its uncertain relation with species presenting the haplotype 2 does not allow enlightening its classification. It could be of interest to enlarge the sample of *D. togoensis* in order to measure the genetic variability of this species before trying to understand its evolution.

Dioscorea bulbifera from the section *Opsophyton* is isolated. It probably diverged early since *D. bulbifera* is a unique species which is present both in Asia and Africa and might have an ancestor who diverged from other *Enantiophyllum* before separation between both continents. *Dioscorea dumetorum* appears as the most distant from the other African species, it is only present in Africa but it belongs to the section *Lasiophyton* that can be found also in Asia or Pacific. The divergence between both sections namely *Enanthiophyllum* and *Lasiophyton* is probably ancient.

Dioscorea preussii is, also, only present in Africa and belongs to section *Macrocarpaea*. It shares alleles with *D. dumetorum* suggesting that both sections have a common ancestor and probably diverged early from section *Enanthiophyllum*.

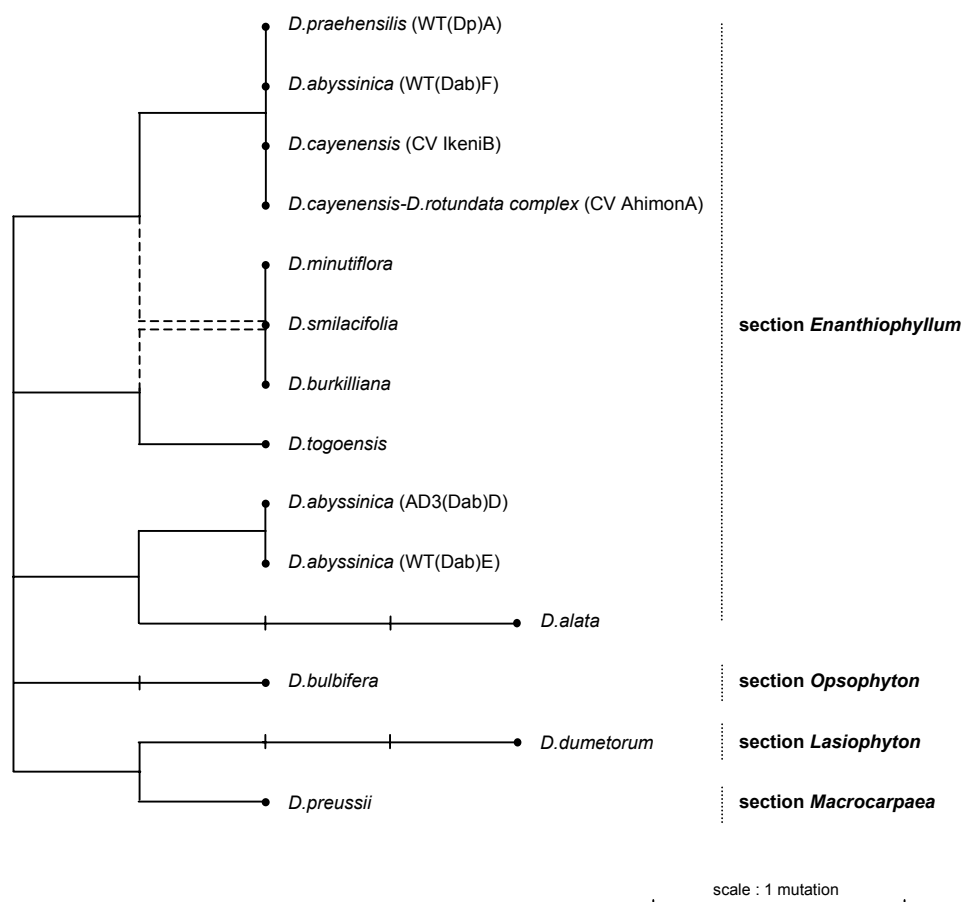


Figure 4: Synthetic representation where haplotypes are illustrated by 14 representatives of species involved in the analysis (dashed lines indicate incompatibility between H1–H2 and H2–H3 clusters). Sections are in bold.

Conclusions

Today, domestication is by far the only way of enrichment of variety portfolios. Because of flowering scarcity of *D. cayenensis-D.rotundata*, it is hard-working to carry out breeding programs on yam. However domestication, a practice mastered by very few farmers, is in the process of disappearance. It took again rise since the researchers have started to be interested in it, by raising the dishonoring character on which it was dependent in some ethnic groups.

But, yam landscape is changing. The access to new varieties is facilitated by the development of road axes and transport. Also because of the shortening of fallow period, the traditional varieties are increasingly abandoned for new varieties more adapted to poor soils (case of *Dioscorea alata*). These changes address double problems i-the abandonment of the domestication which was used by the farmers to supplement their seeds or to try out new genotypes and ii- the abandonment of traditional varieties to the profit of new varieties which is leading to strong genetic erosion.

Research must accompany these changes by trying to preserve farmers' knowledge on domestication and by developing adapted strategies of genetic resource conservation. It

should be accomplished by not only documenting the farmers' knowledge but also by translating them in quantifiable criteria so the domestication could be reproduced by research. This work cannot be complete if a great attention is not paid to the conservation of cultivated varieties and wild types *D. abyssinica* and *D. praehensilis* which according to all recent studies are genetically related.

The goal of our work was to answer the first problem while contributing to translate the criteria of domestication into quantifiable criteria. To be achieved, it should be continued and supplemented with more morphological descriptors and genetic data, in order to be able to reproduce successfully the domestication practice.

References

- Baco, M. N. 2000. La "Domestication" des Ignames Sauvages dans la Sous-Préfecture de Sinendé : Savoirs Locaux et Pratiques Endogènes. Diplôme d'Ingénieur Agronome, Université ationale du Bénin, Abomey-Calavi.
- Bryan, G.J., McNicoll, J., Ramser, G., Meyer, R.C., and DeJong, W.S. 1999. Polymorphic simple sequence repeat markers in chloroplast genomes of Solanaceous plants. *Theor. Appl. Genet.* **99**: 859–867.
- Dumont, R. 1998. Domestication des ignames en Afrique. *In* L'igname, plante séculaire et culture d'avenir. Proceedings of the Séminaire International CIRAD-INRA-ORSTOM-CORAF, Montpellier, France, 3-6 June 1997. *Edited by* J. Berthaud, N. Bricas, and J.-L. Marchand. Montpellier, France. pp. 119–125.
- Hahn, S.K. 1995. Yams. *In* Evolution of crop plants. *Edited by* J. Smartt and N.W. Simmonds Longman. Longman Group, London, U.K. pp. 112–120.
- Hamon, P., Brizard, J.-P., Zoudjihékpon, J., Duperray, C., and Borgel, A. 1992. Étude des index d'ADN de huit espèces d'ignames (*Dioscorea* sp.) par cytométrie en flux. *Can. J. Bot.* **70**: 996–1000.
- Martin, F.W., and Rhodes, A.M. 1977. Intra-specific classification of *Dioscorea alata*. *Trop. Agric. (Trinidad)*, **54**: 1–13.
- Mignouna, H D, and Dansi, A. 2003. Yam (*Dioscorea* ssp.) domestication by the Nago and Fon ethnic groups in Benin. *Genetic Resources and Crop Evolution* **50**:519-528.
- Perrier, X., Flori, A. , Bonnot, F. (2003). Data analysis methods. *In*: Hamon, P., Seguin, M., Perrier, X. ,Glaszmann, J. C. Ed., Genetic diversity of cultivated tropical plants. Enfield, Science Publishers. Montpellier. pp 43 - 76.
- Saitou, N. & M. Nei, 1987. The Neighbor-Joining method: a new method for reconstructing phylogenetic trees. *Mol. Biol. Evol.* **4**: 406–425.
- Scarcelli, N.,Tostain, S.,Mariac, C.,C, AGBANGLA,Dainou, O,J., Berthaud, and Pham, J.L. 2006. Genetic nature of yams (*Dioscorea* sp.) domesticated by farmers in benin (West Africa). *Genetic Resources and Crop Evolution* **53**:121-130.
- Tostain S., N. Scarcelli, P. Bottier, J.L. Marchand, J.L. Pham et J.L. Noyer 2006. Development of DNA microsatellite markers in tropical yam (*Dioscorea* sp.). *Molecular Ecology Notes* **6** : 173–175.
- Vernier, P.,Orkwor, G.C., and Dossou, R. 2003. Studies on yam domestication and farmers' practices in Benin and Nigeria. *Outlook on Agriculture* **32**:35-41.
- Weising, K., and Gardner, R.C. 1999. A set of conserved PCR primers for the analysis of simple sequence repeat polymorphisms in chloroplast genomes of dicotyledonous angiosperms. *Genome*, **42**: 9–19.